

Barth, F. G. and E. -A. Seyfarth 1979. *Cupiennius salei* Keyserling (Araneae) in the highlands of central Guatemala. J. Arachnol., 7:255-263.

CUPIENNIUS SALEI KEYS. (ARANEAE)
IN THE HIGHLANDS OF CENTRAL GUATEMALA

Friedrich G. Barth and Ernst-August Seyfarth

Gruppe Sinnesphysiologie, Fachbereich Biologie
Johann Wolfgang Goethe-Universität
Siesmayerstr. 70
D-6000 Frankfurt a.M., Germany

ABSTRACT

Cupiennius salei Keys. was collected in the highlands of central Guatemala near Cobán (departamento Alta Verapaz). It was found mostly on agaves and on banana plants in coffee plantations near the tropical rain forest. The favorite retreat is at the base of agaves and behind the trough-shaped basal parts of banana leaf sheaths. Showing pronounced rhythmicity in its diurnal locomotor activity, the spider leaves its retreat after dusk to hunt; cockroaches and earwigs were the animals most frequently preyed upon. Included is an account of recent research on this species and of the geographic range and taxonomic placements assigned to it in the literature.

INTRODUCTION

Cupiennius salei Keys. has attained great significance in many aspects of spider research. We know many details about its reproductive and prey catching behavior (Melchers 1963, 1964, 1967), the fine structure of its cuticle (Barth 1969, 1970, 1973), the biochemistry of its hemocyanin and muscle metabolism (Loewe, Linzen and Stackelberg 1970, Loewe and Linzen 1975, Linzen, Angersback, Loewe, Markl and Schmid 1977, Linzen and Gallowitz 1975), the fine structure of its hemocytes and Malpighian tubules (Seitz 1975, 1976), and its embryology and development (Melchers 1963, Seitz 1966, 1967, 1970, 1971). In our own work we have used *Cupiennius* to study strain detection in the exoskeleton by the slit sensilla and the role these organs play in behavior (Barth 1967, 1976, 1978, Barth and Bohnenberger 1978, Bohnenberger 1978, Seyfarth 1978a, b). It has been shown electrophysiologically in this species that the Blumenthal tarsal organ is an odor chemoreceptor (Dumpert 1978).

All these studies were done with offspring bred in the laboratory from animals found in banana shipments of unknown origin (Melchers 1963). There have been no reliable descriptions of the habitat in which *C. salei* lives nor of its behavior in the field except a few, general remarks like those of Vellard (1936).

The growing importance of this species as a laboratory animal warranted a new effort to locate and observe *C. salei* in its natural environment. After reviewing the literature Central America seemed to be the most promising area for a search. In March 1977 we collected *C. salei* in Guatemala. The present paper deals with our field observations and reviews previous reports in the literature on its range and various taxonomic assignments.

OBSERVATIONS

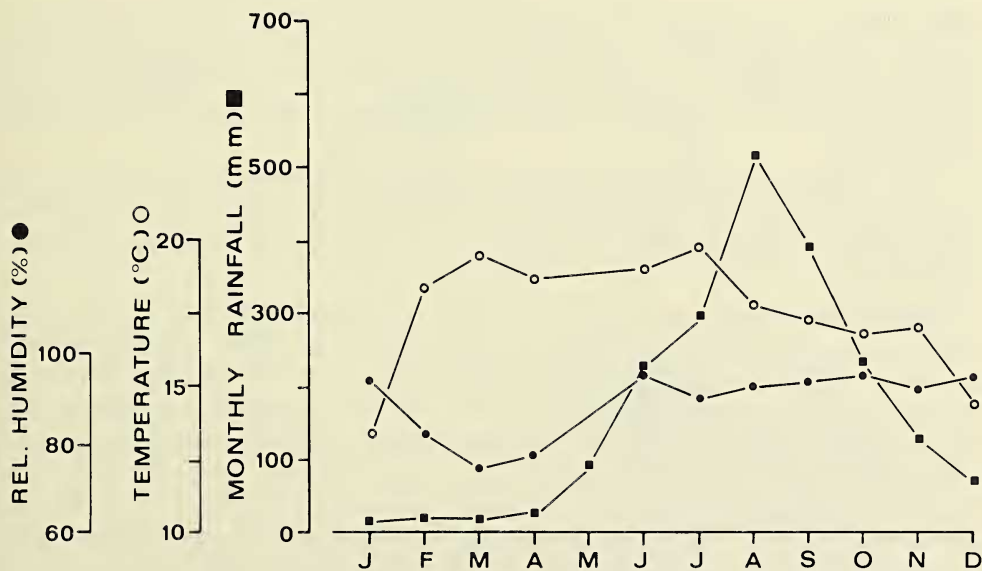
Habitat.—The two areas (Finca Seacté and Finca Remedios) where we found *C. salei* are located in the highlands of central Guatemala in plantations close to Cobán, the capital of the departamento Alta Verapaz (Fig. 1). The elevation of these two places near the neotropical rain forest is 700 and 800 m, respectively. The climate is that of the *tierra templada*: average temperatures range from about 15°C to 20°C with highest readings around May; rainfall is heaviest between August and October, and the dry season lasts from November to about May; the relative humidity is about 90% year round (Fig. 2).

On these plantations banana plants (*Musa sapientum* var. *prusna*) are cultivated as protective shade trees for young coffee plants. Typically *C. salei* lives on these banana plants (Fig. 3). More rarely we found it on agaves (*Furcraea melanodonta* and *Sansevieria* sp.). A few individuals were caught in the immediate vicinity of a finca house in crevices under a tin roof and among a pile of tiles. Young spiders were also found among decaying banana leaves on the ground. Although we searched extensively both during the day and at night we did not find a single individual within the rain forest proper.

Neither banana nor coffee plants, however, are sufficient guides to *C. salei*. We did not find it in the large banana plantations of the warmer lowlands (*tierra caliente*) of the Southwest between Escuintla and San José (departamento Escuintla) nor in the hot and humid area around Flores in the northern lowlands of the Petén. We also searched unsuccessfully in coffee plantations (with banana plants) close to the Lago de Atitlán (departamento Sololá) and on the southern slope of the Volcán de Agua (departamento Escuintla). Likewise, we were unable to find any specimen in Puerto Rico in the Cordillera Central near Maricao or in the Luquillo Mountain Range. Both of these regions belong to the same climatic zone as Alta Verapaz in Guatemala.

A common feature of the plants inhabited by *Cupiennius salei* is the fleshy, mechanically strong character of their leaves and, above all, the trough-like shape of their basal parts, which provide shelters for the spiders. Here they sit prosoma down during the daytime and much of the night (see below) without building any kind of a web. This also applies to females carrying an egg sac. We never found any sort of spider-built retreat. On banana plants the almost closed space formed by the sheaths of outer leaves of the pseudostem is the preferred hiding place (Fig. 3). Here the spiders are protected from direct exposure to sunshine as they are at the base of agaves. Even as late as 11 a.m., when the air temperature had risen to 30°C, spiders in these retreats had their hairy bodies still covered with dew. Some individuals always returned to the same retreat for up to one week, which was the longest period of time we were able to observe at any one location. Others had left their original plants after only one night.

Figure 4 shows the number and distribution of individuals found in the coffee plantation of Finca Remedios close to Tukurú (Fig. 1). We counted 50 individuals in a sample area of 2,750 m² with a total of 131 banana plants. With one exception the 14 individuals found in the leaf litter on the ground were young spiders with a leg span of 6 cm or less, i.e. younger than the eighth moulting stage (Melchers 1963). As a rule the



Figs. 1-2.—Habitat of *Cupiennius salei* Keys. in Guatemala, Central America: 1, location of Finca Seacté and Finca Remedios in the departamento Alta Verapaz; 2, climate of habitat shown by monthly averages of temperature, relative atmospheric humidity, and rainfall. Humidity and temperature values were measured for Finca Seacté in 1975/76, whereas the rainfall data were taken at Finca Remedios and are means for the period from 1972 to 1976.



Fig. 3.—Habitat of *Cupiennius salei* Keys.: Finca Remedios, Alta Verapaz; pseudostems of banana plants within coffee plantation with typical retreats behind leaf sheaths (arrows).

larger stages sat on the pseudostem of the banana plant not more than 1 m above the ground. This corresponds to the observed locations of the retreats behind leaves. Generally we found just one subadult animal at any one time on small agaves and small banana plants, but up to three or four spiders on large plants, usually with one adult among them.

The animals closely match the pattern and coloration given by Melchers (1963), with the exception that adult females tend to be somewhat darker. Since May 1977 we have successfully bred spiders caught in Guatemala with specimens of our original laboratory-raised stock.

Diurnal Rhythmicity.—*Cupiennius salei* has a pronounced diurnal locomotor rhythm (Seyfarth, in prep.). During daytime it is not seen outside its retreat, except occasionally in the very early morning hours. It hunts at night. The onset of locomotor activity is very abrupt. After sunset, at light intensities of about 20 Lux (measured with a calibrated light meter), *C. salei* turns around so that its prosoma points upwards. It remains motionless in this position above its retreat for about half an hour until it is completely dark to the human eye (illumination level below 0.1 Lux). Then the spider starts moving slowly up a leaf to wait for prey. This sequence of events is typical and stereotyped and was seen in many individuals. The time of return to the retreat varies, some spiders being back after three or four hours, others much later. In no case did *C. salei* return immediately after a catch. Instead they fed on their prey wherever they had caught it.

Prey.—The onset of hunting activity in *C. salei* after dusk coincides with the first appearance of a number of potential prey insects like cockroaches, earwigs, flies, crickets,

grasshoppers, and moths. *Cupiennius salei* was seen with specimens of all these insects between its chelicerae, but cockroaches were the prevalent prey in the area studied at that time of the year (March). They were identified as *Epilampra maya* Rehn and *Panchlora* sp., most likely *alcoholua* S.&Z. (Blaberidae), as *Ischnoptera rufa* DeGeer and *Ischnoptera* sp., close to *tolteca* Saussure (Blattellidae). The earwigs preyed upon were *Doru taeniatum* Dohrn (Forficulidae).

The pronounced restriction of hunting activity to the dark period underlines the importance of mechanical signals for prey identification and localization by *C. salei*. Prey is not actively pursued. In general the spider waits motionless until its victim comes within range of a quick and precise jump. It is well known that both air movements and

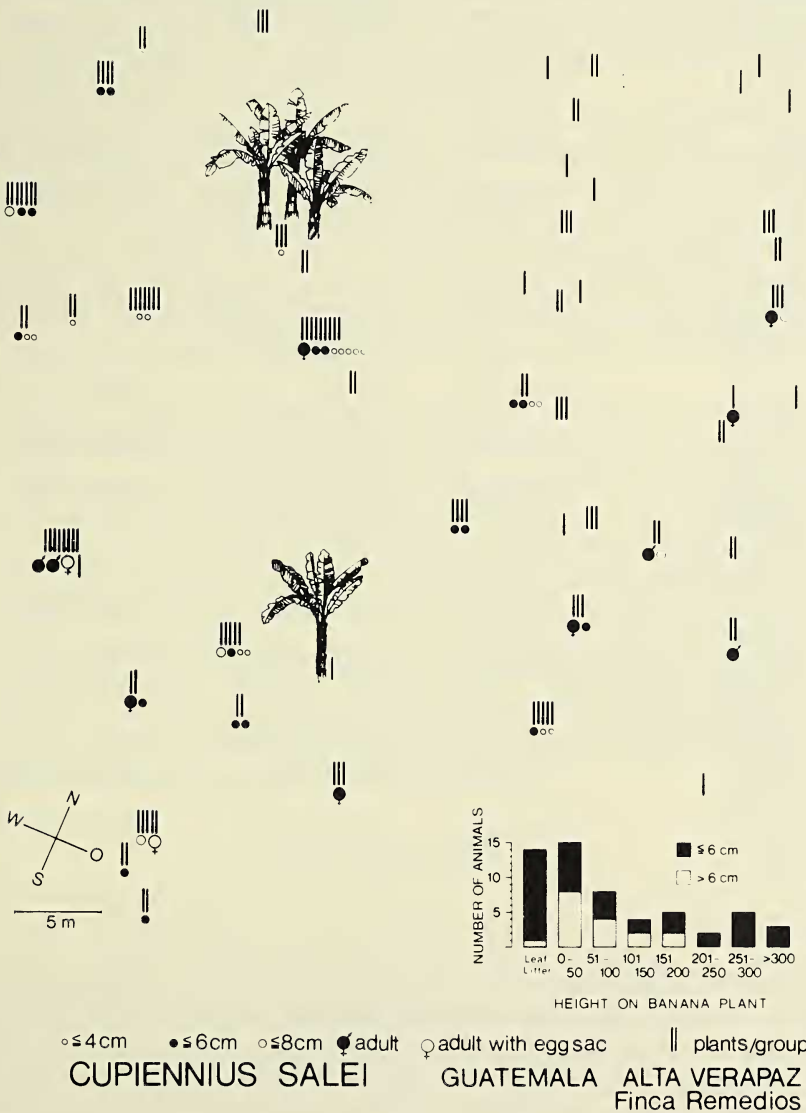


Fig. 4.—Number and distribution of *Cupiennius salei* Keys in a sample area (Finca Remedios) 2,750 m². Vertical bars symbolize banana plants standing either singly or in groups. Vertical distribution of animals is shown by graph on lower right.

Table 1.—Summary of reports on *Cupiennius salei* Keys., including synonymies, taxonomic assignments, and geographic range. Only such sources listed which state or imply that specimens were newly collected. Therefore accounts such as Comstock (1912), Mello-Leitão (1936), Bonnet (1945), and Levi et al. (1968) not included here. An asterisk (*) indicates family assignment used for the first time.

BINOMIAL	FAMILY	ORIGIN	AUTHOR
1. <i>Ctenus</i> <i>salei</i> n.sp.	* Ctenoidae	South America Mexico (Veracruz)	Keyserling (1877)
2. <i>Phoneutria</i> <i>oculifer</i> n.sp.	* Ctenidae	Mexico	Karsch (1879)
3. <i>Cupiennius</i> <i>oculatus</i> n.sp.	* Clubionidae	Guatemala	Simon (1891, 1897)
4. <i>Ctenus</i> <i>mordicus</i> n.sp.	Ctenidae	Guatemala (Salinas de Nueve Cerros)	O. P.-Cambridge (1892)
5. <i>Ctenus</i> <i>salei</i> Keys. <i>Cupiennius</i> <i>oculatus</i> Simon	"Cteniform"	Guatemala, South America, Mexico	F.O.P.-Cambridge (1897)
6. <i>Cupiennius</i> <i>sallei</i> Keys.	* Pisauridae	Mexico, Guatemala, Honduras, Costa Rica, Panama	F.O.P.-Cambridge (1901)
7. <i>Cupiennius</i> <i>sallei</i> Keys.	Ctenidae	Florida (Lake Worth)	Banks (1904)
8. <i>Cupiennius</i> <i>sallei</i> Keys.	Pisauridae	Costa Rica (Surubres, 250 m)	Banks (1909)
9. <i>Cupiennius</i> <i>sallei</i> Keys. = <i>Phoneutria</i> <i>oculifera</i> Karsch	Pisauridae	Brasil (Pará) Rio Hondo (?)	Strand (1910)
10. <i>Cupiennius</i> <i>sallei</i> Keys.	Ctenidae	Panama	Petrunkevitch (1925)
11. <i>Cupiennius</i> <i>sallei</i> Keys.	Pisauridae	Mexico (Veracruz)	Roewer (1933)
12. <i>Cupiennius</i> <i>sallei</i> Keys.	Ctenidae	Panama (Barro Colorado Island)	Chickering (1936)
13. <i>Cupiennius</i> <i>sallei</i> Keys.	Pisauridae	Guatemala	Schmidt (1954)
14. <i>Cupiennius</i> <i>sallei</i> Keys.	* Lycosidae	Laboratory-bred	Homann (1971)

substrate-carried vibrations caused by potential prey are the signals decisive for prey detection. Measurements with a capacitive transducer probe show that vibration signals caused by prey and carried across an agave leaf remain strong enough to be detected by a *Cupiennius* sitting at least 20 cm away from the vibration source. Comparable results are expected with the banana pseudostem. The frequency power spectrum contained in such natural vibrations is characterized by low frequencies with a maximum below 30 Hz (Barth, in prep.).

DISCUSSION

Apparently the chief climatic requirements of *C. salei* are moderate daytime temperatures (approximately 25°C) and a high degree of humidity (see also Melchers 1963a). Both conditions prevail in the observed, typical retreats behind leaves of banana stems or at the base of agaves. Concurrently these plants are a substrate for prey catching. *Cupiennius salei* hunts at night, thus again behaviorally avoiding the heat extremes. Actograph measurements as well show that it restricts its locomotor activity to the dark period of the day (Seyfarth, in prep.). We therefore assume that normally also searching for sexual partners, mating, and moulting take place during the night. Although we did not find *C. salei* in the tropical rain forest adjoining the plantations, we do not exclude the possibility that the species inhabits suitable forest plants like epiphytic bromeliads. Obviously *C. salei* did not evolve in plantations and in fact Chickering (1936) reports it as occurring in the forests of Barro Colorado Island, Panama.

Table 1 summarizes previous reports on the origins and range of *C. salei*. The findings in Mexico, Guatemala, Costa Rica, and Panama are comparatively well documented, but characterizations of the various habitats are lacking in all cases. The report of a *Cupiennius* found in Florida (Banks, 1904) is apparently based on a single specimen; most of the *Cupiennius* in the Harvard collection were found in fruit stores of the eastern USA, i.e. were introduced to the USA in fruit shipments from abroad. We conclude that *C. salei* lives throughout Central America, possibly including some Caribbean islands, but is unlikely to occur in the continental USA or South America (pers. comm. with local arachnologists).

There is also no general agreement on the systematic position of *C. salei*. In order to stimulate taxonomic work with this widely used laboratory spider, we have also included in Table 1 the variety of names and taxonomic assignments given to the species. Although we presently do not contribute new data to the controversy of the systematic position of *Cupiennius* we particularly want to draw attention to the work of Homann (1961, 1966, 1971, 1975), who has included *C. salei* in his comparative studies. According to Homann the Lycosidae, Pisauridae, and Ctenidae cannot be separated from each other as families. In a way this statement mirrors the fact that in the previous literature all three families are offered for *Cupiennius*. Homann considers them subfamilies (Lycosinae, Pisaurinae, Cteninae) of the Lycosidae. Among several arguments he stresses similarities of eye anatomy and ontogeny. All the above "lycosids" have three pairs of secondary eyes with a grate-shaped tapetum and rhabdoms arranged in rows.

ACKNOWLEDGMENTS

This study was supported by a grant from the Deutsche Forschungsgemeinschaft (Ba 304/8). Dr. G. Kramer generously shared her intimate knowledge of Guatemala and provided the humidity and temperature data for Finca Seacté. We appreciate the effective help of the German Embassy in Guatemala City and are particularly grateful to Mr. A. Schleeauf and Mr. R. Schleeauf for their hospitality and permission to work on their plantations. Mr. A. Schleeauf kindly provided the rainfall data for Finca Remedios. We are also indebted to Dr. A. Brindle, Manchester Museum, and to Dr. A. Gurney, Systematic Entomology Laboratory, Washington, D.C., for kindly identifying the earwigs and the cockroaches.

LITERATURE CITED

- Banks, N. 1904. The arachnida of Florida. Proc. Acad. Nat. Sci. Philadelphia, 56: 120-147.
- Banks, N. 1909. Arachnida from Costa Rica. Proc. Acad. Nat. Sci. Philadelphia, 61: 194-234.
- Barth, F. G. 1967. Ein einzelnes Spaltsinnesorgan auf dem Spinnentarsus: seine Erregung in Abhängigkeit von den Parametern des Luftschallreizes. Z. vergl. Physiol., 55: 407-449.
- Barth, F. G. 1969. Die Feinstruktur des Spinnenintegumentes. I. Die Cuticula des Laufbeins adulter häutungsferner Tiere (*Cupiennius salei* Keys.). Z. Zellforsch., 97: 137-159.
- Barth, F. G. 1970. Die Feinstruktur des Spinnenintegumentes. II. Die räumliche Anordnung der Mikrofaseren in der lamellierten Cuticula und ihre Beziehung zur Gestalt der Porenkanäle (*Cupiennius salei* Keys., adult, häutungsfern, Tarsus). Z. Zellforsch., 104: 87-106.
- Barth, F. G. 1973. Laminated composite material in biology. Microfiber reinforcement of an arthropod cuticle. Z. Zellforsch., 144: 409-433.
- Barth, F. G. 1976. Sensory information from strains in the exoskeleton, Pp. 445-473, *In* The insect integument, H. R. Hepburn (ed.). Elsevier Sci. Publ. Co., Amsterdam, Oxford, New York.
- Barth, F. G. 1978. Slit sense organs: "Strain gauges" in the arachnid exoskeleton. Symp. zool. Soc. London, 42: 439-448.
- Barth, F. G. and J. Bohnenberger. 1978. Lyriform slit sense organ: threshold and stimulus amplitude ranges in a multi-unit mechanoreceptor. J. comp. Physiol., 125: 37-43.
- Bohnenberger, J. 1978. On the transfer characteristics of a lyriform slit sense organ. Symp. zool. Soc. London, 42: 449-455.
- Bonnet, P. 1945. Bibliographia Araneorum. II. Douladore, Toulouse, France.
- Chickering, A. M. 1936. Additions to the list of known species of spiders from Barro Colorado Island, Panama. Trans. Amer. Micr. Soc., 55: 449-456.
- Comstock, J. H. 1912. The spider book. Doubleday, Doran & Co., Inc., New York.
- Dumpert, K. 1978. Spider odor receptor: Electrophysiological proof. Experientia, 34: 754-755.
- Homann, H. 1961. Die Stellung der Ctenidae, Tetricinae und Rhoicininae im System der Araneae. Senck. biol., 42: 401-402.
- Homann, H. 1966. Augen und Systematik bei den Araneae (Arachnida). Senck. biol., 47: 63-66.
- Homann, H. 1971. Die Augen der Araneae. Anatomie, Ontogenie und Bedeutung für die Systematik. Z. Morph. Tiere, 69: 201-272.
- Homann, H. 1975. Die Stellung der *Thomisidae* und der *Philodromidae* im System der Araneae (Chelicerata, Arachnida). Z. Morph. Tiere, 80: 181-202.
- Karsch, F. 1879. Westafrikanische Arachniden. Z. ges. Naturw., 52: 329-373.
- Keyserling, Graf E. 1877. Ueber amerikanische Spinnenarten der Unterordnung *Citigradae*. Verh.d.k.k. Zool. Bot. Ges., 26: 609-708.
- Levi, H. W., L. R. Levi, and H. S. Zim. 1968. Spiders and their kin. Western Publ. Co., Inc., New York.
- Linzen, B. and P. Gallowitz. 1975. Enzyme activity patterns in muscles of the lycosid spider, *Cupiennius salei*. J. comp. Physiol., 96: 101-109.
- Linzen, B., D. Angersbach, R. Loewe, J. Markl, and R. Schmid. 1977. Spider hemocyanins: Recent advances in the study of their structure and function, Pp. 31-36, *In* Structure and function of haemocyanin, J. V. Bannister (ed.). Springer-Verlag, Berlin, New York, Heidelberg.
- Loewe, R., B. Linzen, and W. Stackelberg. 1970. Die gelösten Stoffe in der Hämolymphe einer Spinne, *Cupiennius salei* Keyserling. Z. vergl. Physiol., 66: 27-34.
- Loewe, R. and B. Linzen. 1975. Haemocyanins in spiders. II. Automatic recording of oxygen binding curves, and the effect of Mg^{++} on oxygen affinity, cooperativity, and subunit association of *Cupiennius salei* haemocyanin. J. comp. Physiol., 98: 147-156.
- Melchers, M. 1963a. Zur Biologie und zum Verhalten von *Cupiennius salei* (Keyserling), einer amerikanischen Ctenide. Zool. Jb. Syst., 91: 1-90.
- Melchers, M. 1963b. *Cupiennius salei* (Ctenidae). Kokonbau und Eiablage. Encyclopaedia Cinematographica. G. Wolf (ed.). E 363: 1-10. Inst. wiss. Film, Göttingen.
- Melchers, M. 1963c. *Cupiennius salei* (Ctenidae). Spinnhemmung beim Kokonbau. Encyclopaedia Cinematographica. G. Wolf (ed.). E 364: 1-6. Inst. wiss. Film, Göttingen.
- Melchers, M. 1963d. *Cupiennius salei* (Ctenidae). Einspinnen der Beute und Nahrungsaufnahme. Encyclopaedia Cinematographica. G. Wolf (ed.). E 421: 1-6. Inst. wiss. Film, Göttingen.

- Melchers, M. 1963e. *Cupiennius salei* (Ctenidae). Putzen. Encyclopaedia Cinematographica. G. Wolf (ed.). E 422: 1-7. Inst. wiss. Film, Göttingen.
- Melchers, M. 1964. *Cupiennius salei* (Ctenidae). Häutung. Encyclopaedia Cinematographica. G. Wolf (ed.). E 724: 1-11. Inst. wiss. Film, Göttingen.
- Melchers, M. 1967. Der Beutefang von *Cupiennius salei* Keyserling (Ctenidae). Z. Morph. Okol. Tiere, 58: 321-346.
- Mello-Leitão, de C. 1936. Contribution à l' étude des Ctenides du Brésil. Festschr. Strand, 1: 1-31.
- Petrunkévitch, A. 1925. Arachnida from Panama. Trans. Connecticut Acad. Arts. Sci., 27: 51-248.
- Pickard-Cambridge, F. O. 1892. Arachnida, Araneida and Opiliones, *In Biologia Centrali-Americana*. I. Dulau and Co., London.
- Pickard-Cambridge, F. O. 1897. On cteniform spiders from the lower Amazonas and other regions of North and South America, with list of all known species of these groups hitherto recorded from the New World. Ann. Mag. Nat. Hist., 19: 52-106.
- Pickard-Cambridge, F. O. 1901. Arachnida, Araneida and Opiliones. *In Biologia Centrali-Americana*. II. Dulau and Co., London.
- Roewer, C. F. 1933. Araneen aus mexikanischen Ameisenwohnpflanzen. Zool. Anz., 102: 183-188.
- Schmidt, G. 1954. Zur Herkunftsbestimmung von Bananenimporten nach dem Besatz an Spinnen. Z. ang. Ent., 36: 400-422.
- Seitz, K. A. 1966. Normale Entwicklung des Arachniden-Embryos *Cupiennius salei* Keyserling und seine Regulationsbefähigung nach Röntgenbestrahlung. Zool. Jb. Anat., 83: 327-447.
- Seitz, K. A. 1967. Untersuchungen über dynamische Vorgänge im Ei der Spinne *Cupiennius salei* (Ctenidae) mittels Röntgen-Barrieren. Zool. Jb. Anat., 84: 343-374.
- Seitz, K. A. 1970. Embryonale Defekt- und Doppelbildungen im Ei der Spinne *Cupiennius salei* (Ctenidae). Zool. Jb. Anat., 87: 588-639.
- Seitz, K. A. 1971. Licht- und elektronenmikroskopische Untersuchungen zur Ovarentwicklung und Oogenese bei *Cupiennius salei* Keys. (Araneae, Ctenidae). Z. Morph. Tiere, 69: 283-317.
- Seitz, K. A. 1975. Licht- und elektronenmikroskopische Untersuchungen an den Malpighischen Gefäßen der Spinne *Cupiennius salei* Keys. (Ctenidae, Araneae). Zool. Jb. Anat., 94: 413-440.
- Seitz, K. A. 1976. Zur Feinstruktur der Häutungshämocyten von *Cupiennius salei* Keys. (Araneae, Ctenidae). Zool. Jb., 96: 280-292.
- Seyfarth, E.-A. 1978a. Lyriform slit sense organs and muscle reflexes in the spider leg. J. Comp. Physiol., 125: 44-57.
- Seyfarth, E.-A. 1978b. Mechanoreceptors and proprioceptive reflexes: Lyriform organs in the spider leg. Symp. zool. Soc. London, 42: 457-467.
- Simon, E. 1891. Descriptions de quelques arachnides du Costa-Rica, communiqués par M. A. Getax (de Genève). Bull. Soc. Zool. France, 16: 109-112.
- Simon, E. 1897-1903. Histoire naturelle des Araignées. II. Encyclopédie Roret, Paris.
- Strand, E. 1910. Neue oder wenig bekannte neotropische cteniforme Spinnen des Berliner Museums. Zool. Jb. Syst., 28: 401-428.
- Vellard, J. 1936. Le venin des araignées. Monogr. de l' Institut Pasteur. Masson et Cie., Paris.